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DOI:
10.1002/eco.1982

Received: 14 October 2017 | Revised: 6 March 2018 | Accepted: 26 March 2018

DOI: 10.1002/eco.1982

RESEARCH ARTICLE

WILEY

Spatio-temporal dynamics of macroinvertebrate communities in northeast Greenlandic snowmelt streams

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Funding information
Carlsberg Foundation, Grant/Award Number: 2013-01-0258; European Union Seventh Framework Programme, Grant/Award Number: 262693; Natural Environment Research Council, Grant/Award Number: NE/L501712/1

Abstract

Future climate change throughout the Arctic is expected to increase channel stability in glacially influenced streams through reduced contributions from glacial meltwater and increases in groundwater. In contrast, predictions for northeast Greenland of increased precipitation for the next 100 years—including winter snowfall—which with warmer air temperature, is expected to increase the size of spring floods in snowmelt streams. Coupled with increased disturbance through frequent summer rainfall events, nivation processes and permafrost degradation will reduce resistance of channel sediments to erosion and thereby decrease channel stability. Decreased channel stability will impact macroinvertebrate abundance and diversity. Five streams sourced by snowpacks of varying extent were studied over 3 summer seasons (2013–2015) to investigate the potential effect of shift in snowmelt regime on macroinvertebrate communities.

Total abundance and taxa richness were significantly higher in streams with small snowpacks, where the chironomid genus *Hydrobaenus* was the most abundant taxon. Streams with large snowpacks were dominated by the chironomid genus *Diamesa*. Multivariate ordination models and correlation indicated that macroinvertebrate communities were significantly influenced by channel stability and bed sediment size. Macroinvertebrate abundance was significantly higher in 2013, following low winter snowfall and associated low meltwater inputs to streams, highlighting interannual variability in macroinvertebrate communities.

A shift towards less stable habitats in snowmelt streams will potentially lead to reduced macroinvertebrate abundance and taxa richness, and local extinction of specialized taxa. Thus, snowmelt-fed streams in northeast Greenland may respond very differently to changing climate compared with streams in parts of the Arctic dominated by glacial meltwater.

KEYWORDS

Arctic, channel stability, Chironomidae, climate change, freshwater, hydroecology, meltwater, snow

1 | INTRODUCTION

Climate change is expected to cause large shifts in Arctic ecosystems (Anisimov et al., 2007; Prowse et al., 2009; Prowse, Furgal, Wrona, & Reist, 2009; Walsh et al., 2005), with some of the most pronounced changes in northeast Greenland (Stendel, Christiansen, & Petersen, 2008). Air temperature in the region is predicted to increase and due to the reduction in regional sea ice extent, local surface evaporation will result in increased precipitation by up to 60%, falling as rain in summer and snow in winter (Bintanja & Selten, 2014; Stendel et al., 2008). These changes will shift local climatic conditions from a continental high-Arctic climate towards an increasingly maritime low-Arctic climate with a marked influence on freshwater ecosystems in this region.

Glacial meltwater is currently the principal meltwater source for streams in many regions of the high Arctic. Climate change will lead to reduced extent of glaciers, which, although for larger glaciers runoff will initially increase in the near term, will in the long term or for smaller glaciers lead to decreased glacial runoff and groundwater, becoming a more dominant water source as the active layer deepens (e.g., Blaen, Brown, Hannah, & Milner, 2014; Hannah et al., 2007; Milner, Brown, & Hannah, 2009). These changes are predicted to increase channel stability and water temperature, leading to increased macroinvertebrate density and alpha diversity (Blaen et al., 2014; Brown, Hannah, & Milner, 2007; Lods-Crozet, Lencioni, Brittain, Marziali, & Rossaro, 2007; Milner et al., 2009). However, in areas of low glacial cover such as coastal northeast Greenland, the predicted increases in snowfall (Collins et al., 2013; Kattsov et al., 2007) means increased snow meltwater contributions to streams, alongside increased summer rainfall events. These snowmelt inputs to streams will have both a more prolonged impact on streams throughout the summer due to the longer time required for snowpack melting and also increased inputs to streams during days with high air temperature. The absence of predictable summer glacier melt, as evident in glacially dominated systems, increases flow stochasticity with high short-term variability in magnitude and duration (Milner et al., 2017). Snowpacks can have a large influence on local geomorphology dependent upon their size through a variety of processes, influencing permafrost thaw by insolating ground from cold air temperature (Westermann et al., 2015), causing large spring floods that destabilize stream bank sediment, and by triggering a range of nivation processes, such as pronival solifluction, backwall failure, and accumulation of alluvial fans and basins (Christiansen, 1998), with larger snowpacks potentially having the largest impact. These processes can lead to increased sediment fluxes and solute inputs into stream systems (Buffam, Laudon, Temnerud, Mörth, & Bishop, 2007; Chin, Culp, Lacelle, & Kokelj, 2016; Christiansen, 1998; Kokelj et al., 2013; Kokelj et al., 2015; Malone, Lacelle, Kokelj, & Clark, 2013; Moiseenko, Kudrjavezeva, & Rodyshkin, 2001) and increase stream channel mobility, thereby overall lowering channel stability. As a result, increased snowfall in northeast Greenland could lead to negative consequences for benthic communities with reduced macroinvertebrate abundance and diversity. This outcome contrasts to general predictions of increased channel stability in glacially dominated Arctic streams in a warmer future due to reduced glacial meltwater contributions. Also, interannual variation in snowfall conditions, as currently seen in the region (Pedersen et al., 2016), would combine with increased frequency of heavy summer rainfall events and together could lead to variation in macroinvertebrate community structure between years due to an increase in extreme events, varying habitat conditions, and disturbance regimes. Stream studies on increased thermokarst activity in Arctic Canada indicated that high sediment load from increased channel disturbance can cause decreased macroinvertebrate community complexity in streams (Chin et al., 2016) by reducing habitat availability, altering water chemistry and causing negative physiological impacts such as the clogging of feeding and respiratory organs (Jones, Duerdoth, Collins, Naden, & Sear, 2012; Lemly, 1982). However, although this has been tested for thermokarst activity, this has not been tested in relation to the overall effect of climate change on snowmelt-dominated Arctic streams.

Previous river research in northeast Greenland has largely been restricted to hydrological research on sediment and solute transport dynamics (Hasholt et al., 2008; Hasholt & Hagedorn, 2000; Ladegaard-Pedersen et al., 2016; Rasch, Elberling, Jakobsen, & Hasholt, 2000; Søndergaard et al., 2015), whereas ecological studies in freshwater systems have been principally restricted to lakes and ponds (e.g., Christoffersen, Amsinck, Landkildehus, Lauridsen, & Jeppesen, 2008). River ecology research in Greenland has been limited to the more accessible southwest coast (Friberg, Milner, Svendsen, Lindegaard, & Larsen, 2001; González-Bergonzoni et al., 2014), thus our understanding of stream ecology along the east coast is negligible. The northeast coast of Greenland is more isolated than the west, and is thought to have reduced macroinvertebrate diversity due to its northern latitude, its recent deglaciation, and its biogeographical isolation between the Greenland ice sheet and the ocean where harsh environmental conditions and large distances restrict invertebrate dispersal routes (Böcher, Kristensen, Pape, & Vilhelmsen, 2015). Documenting the species present in this region will provide a vital record to monitor change in stream ecosystems over the coming decades.

Here, we investigate the influence of climate change on stream ecosystems in northeast Greenland by undertaking an analogous study of streams sourced by snowpacks of varying extents, representing different snowpack conditions. The aim of this study was to investigate the influence of disturbance regimes associated with different snowpack conditions on macroinvertebrate community composition. To meet the aim, we tested the following hypotheses: (1) streams sourced from larger snowpacks will have reduced channel stability; (2) streams with lower channel stability will have lower macroinvertebrate taxa richness, diversity, and abundance; and (3) higher interannual variability in macroinvertebrate community will be related to size of the snowpack. From this, indicator taxa for different stream ecosystems will be determined, and results were compared with other areas of Greenland and the wider Arctic in order to explore the implications of climate change for Arctic snowmelt streams.

2 | METHODS

2.1 | Study site

Five streams were selected for study in close proximity to Zackenberg research station (74°28′ N, 20°34′ W) located within the Northeast Greenland National Park in the high Arctic climatic zone (Figure 1). Fieldwork was undertaken between June 25–July 17, 2013, July 1–22, 2014, and July 6–22, 2015. The field site was located 70 km from the Greenland ice sheet, and was not hydrologically connected to it.

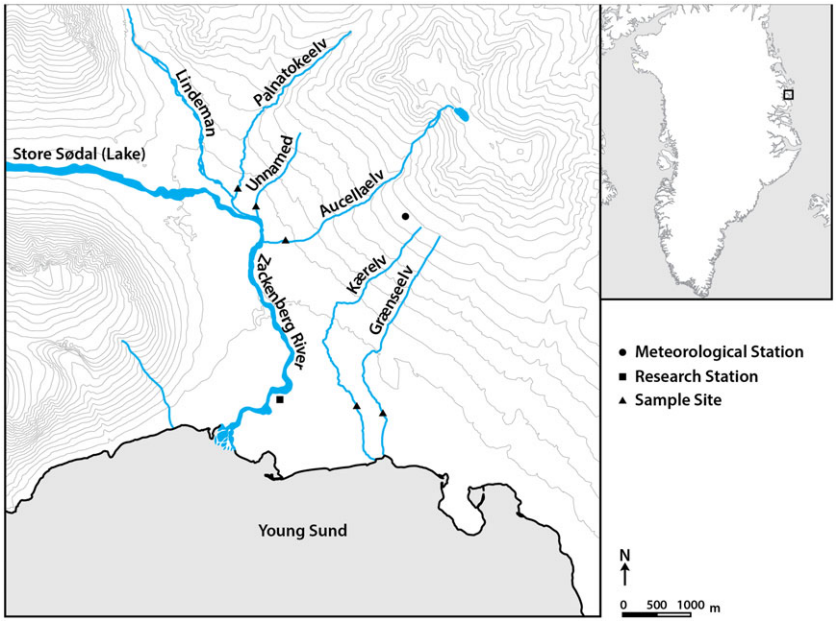

FIGURE 1 Map of study area showing the five study streams and their location in Northeast Greenland

Mean annual air temperature is −9.1 °C with July being the warmest month with a mean air temperature of 5.8 °C. Annual mean precipitation is 261 mm and falls predominantly as snow (Hansen et al., 2008).

Altitude in the region varies between sea level and 1,450 m a.s.l. and the lowlands are characterized by a wide valley created through glacial erosion (Mernild, Liston, & Hasholt, 2007). AP Olsen ice cap is within the catchment of Zackenberg river, and a few high-altitude glaciers remain within the area. All sample sites were located on the valley floor, which is characterized by continuous permafrost with an active layer depth varying between 0.3 and 0.65 m (Christiansen, Sisgaard, Humlum, Rasch, & Hansen, 2008). All streams were overlying a combination of cretaceous and tertiary sandstones, with upper reaches overlying conglomerates, black shale, and basalts. The valley floor and low altitude slopes were characterized by a layer of loose soils that were vulnerable to erosion, even though soils were well developed in areas (Hasholt & Hagedorn, 2000; Mernild et al., 2007). Lowland vegetation in this region comprised *Cassiope tetragona* heaths with *Salix arctica*, and grasslands, fens, and snowbeds were characteristic of this area (Bay, 1998).

Snow was the principal water source for all study streams. Aucellaelv and Palnatokeelv also received small glacier meltwater contributions, but this was minimal during the field period and they would be classed as nival streams as defined by Brown, Hannah, and Milner (2003). Streams are sourced from snowpacks of varying sizes. Aucellaelv (N74.49 4062°–20.575144°) and Palnatokeelv (N74.510095°–20.602894°) were characterized by large, perennial snowpacks, the principal snowpack for Unnamed (N74.506048°–20.585924°) was small, however, it also received inputs from larger perennial sources, whereas smaller, seasonal snowpacks that typically melted by the end of the summer season were found at Kærlev (N74.471039°–20.519908°) and Grænseelv (N74.468211°–20.497409°).

2.2 | Environmental habitat conditions

Air temperature, snow depth, and precipitation data were obtained from a weather station located within 5 km of all sites maintained by the Greenland Ecosystem Monitoring Programme. Air temperature and snow depth were measured half-hourly and precipitation was measured hourly. Habitat condition was monitored and data were collected simultaneously to macroinvertebrate collection. The Pfankuch Index was calculated for each site to determine channel stability (Pfankuch, 1975) using all three components of the index (upper banks, lower banks, and stream bed). Higher Pfankuch Index values correspond to lower channel stability. Water samples were collected to analyse for major ions and nutrients. Samples were filtered in the field using Whatman GF/F paper and frozen within 6 hr of collection until analysis could take place. NH_4^+, NO_3^-, and PO_4^{3-} were analysed using the hypochlorite, cadmium reduction, and ascorbic acid methods, respectively, on a Lachat QuikChem flow injection analyser (Lachat Instruments, APC Bioscientific Limited, England; APHA, 2012). To determine suspended sediment, 1 L water samples were collected from each stream and filtered onto preweighed GF/F papers in the laboratory. These were then dried at 60 °C for 48 hr, before being reweighed to calculate suspended sediment concentration. Water temperature, conductivity, and pH were measured as spot tests using a waterproof HI-98129 Pocket EC/TDS and pH Tester (Hanna meter). Water depth was measured every 0.2 m and average water depth was calculated. To calculate average bed sediment size (D_{50}), 100 randomly selected stones were measured along the B axis. Chlorophyll *a* (Chl *a*) was measured as a proxy for benthic algal biomass. Five stone samples with a B axis of over 6 cm were selected for benthic algae measurements. Biofilm was removed from substrate using a toothbrush and collected on a Whatman GF/C filter. In the laboratory, filter papers were submerged in 96% ethanol and absorbance was measured at 665 and 750 nm on a spectrophotometer (UV 1700 Spectrophotometer, Shimadzu, Japan). Chl *a* biomass was calculated as Chl $a = (Abs_{665} - Abs_{750}) * E / 83.4 * A * 10^{-4}$, where E is the volume of ethanol (ml), 83.4 is the absorption of Chl *a* in ethanol, A is the sample area (cm^2), and 10^{-4} is the conversion factor (cm^2 to m^2; Steinman, Lamberti, & Leawitt, 2007) in order to compare on the same scale as macroinvertebrates.

2.3 | Macroinvertebrate community structure

Macroinvertebrates were collected each year using five replicate samples with a Surber sampler (0.093 m^2 and 300 μm mesh size) in the same 20 m reach. Samples were preserved in 90% ethanol in Whirlpak bags. In the laboratory, samples were sieved through a 200 μm sieve and sorted under 10× magnification. Chironomids with dark head capsules were immersed in 10% potassium hydroxide (KOH) solution on a hot plate at 60 °C for 15 min to lighten the head capsule and to make characteristic features easier to see. Chironomids and Ceratopogonindae were then mounted on slides using DMFH mountant. Chironomidae were identified to species-type or the lowest taxonomic level possible using the following keys: Cranston (1982), Wiederholm (1983), Brooks, Langdon, and Heiri (2007), Ferrington and Sæther (2011), and Lindegaard (2015). Other macroinvertebrates were identified to the lowest level possible using the keys Nilsson (1996) and Dobson (2013).

2.4 | Data analysis

Time series were constructed to show air temperature and precipitation throughout the three field campaigns and snow depth variation over the 3 years. One-way and two-way ANOVAs were conducted to determine significant differences in environmental variables between sites and years. Significant results were then subjected to Tukey HSD post hoc tests to determine significantly different pairs. All statistically significant pairings were reported. Previous to analysis, normality of data was tested using Levenes test and residual plots. Non-normally distributed data were log10 transformed before analysis.

Data from macroinvertebrate samples were used to determine the community metrics: abundance, Shannon diversity, taxa richness, and evenness to quantify how equal the community is numerically. The difference in community metrics between years was calculated to show interannual variation between sites. The ratio of Diamesa to Orthocladiinae was calculated for each site and year.

Differences in macroinvertebrate community metrics between streams and years were investigated by two-way ANOVA and Tukey post hoc tests where abundance data were log10(x + 1) transformed following standard procedure and to make comparable with other studies. Similar to the environmental variables, data were first tested for normality using Levenes test and residual plots. To determine the correlation between different environmental variables and community metrics, Spearman's rank correlation coefficient was conducted. Spearman's Rank was used due to the small size of the data set and potential for non-linear relationships (Zar, 2010).

The relationship of macroinvertebrate community assemblages to habitat variables was examined using nonmetric multidimensional scaling (NMDS) as a two-dimensional ordination plot. Previous research indicates adding more dimensions only minimally reduces stress (Soininen, 2004). The ordination was compiled using Bray Curtis dissimilarities after 999 permutations to avoid the risk of local optima (Soininen, 2004) and macroinvertebrate abundance data were log10(x + 1) transformed prior to use. Environmental variables were also log10(x + 1) transformed and fitted in the ordination using 119 permutations. The environmental variables significantly correlated with the ordination plot were added to the ordination space.

To investigate taxa similarity between study sites, a two-way cluster analysis was constructed in the PAST software using the paired-group method with Bray Curtis similarity index on log10(x + 1) transformed data. Taxa were clustered by abundance in different streams and sites were clustered by taxa abundance. Rare species (<5%) were excluded to avoid their large influence on the analysis (Niedrist & Füreder, 2016). The labdsv function in the R environment was used to determine indicator species for specific habitats, where the given indicator value is a function of frequency and mean abundance of species in specific classes, and the *p* value provided indicates the probability of finding higher indicator values under random permutations where low probability gives a significant value ($p < .05$; Oksanen, 2014). Species with indicator value of 95% or higher are presented.

3 | RESULTS

3.1 | Environmental habitat conditions

Weather conditions over the three field campaigns varied markedly with 2014 characterized by two large rain storm events (total precipitation: 37.6 mm). The 2013 field campaign was characterized by small rainfall events (total precipitation: 8.8 mm), whereas the 2015 field campaign was comparatively dry (total precipitation: 0.4 mm; Figure 2). The highest mean air temperatures were during the 2015 field campaign at 7.1 °C, whereas mean air temperatures were very similar during the 2013 (5.9 °C) and 2014 (6.0 °C) field campaigns (Figure 2). Snow depth was highly variable during the winters previous to sampling. Winter 2012–2013 (September–June) saw very low snow fall (maximum snow depth of 0.16 m) compared with winter 2013–2014 (0.91 m) and winter 2014–2015, which saw high snow accumulation (1.44 m; Figure 3).

Environmental variables showed marked variation between streams and between years. Channel stability was significantly higher in Kærelv and Grænseelv than in Unnamed, Aucellaelv and Palnatokeelv ($F(1,4) = 417.63$, $p < .001$) with significantly smaller bed sediment size ($F(1,4) = 48.83$, $p < .01$). Suspended sediment was substantially higher in Aucellaelv and Palnatokeelv compared with Kærelv, Grænseelv, and Unnamed (Table 1). Conductivity was significantly higher in 2013 compared with 2014 and 2015 ($p < .01$). No significant variation was found in NH_4^+ or PO_4^{3-} but NO_3^- varied between sites and years, with higher NO_3^- concentrations in Aucellaelv than Kærelv and Grænseelv, although not significantly different ($p = .06$, $p = .055$, respectively). Ca and Mg concentrations showed significant variation between years (see Tables 2 and 3). Ca concentration was significantly higher in Unnamed than in Palnatokeelv ($p < .05$) and was significantly higher in 2013 compared with 2014 and 2015 (both: $p < .01$). Mg concentrations were significantly higher in Aucellaelv compared with Kærelv and Palnatokeelv, and in 2013 compared with 2014 ($p < .05$) and 2015 ($p < .01$). Two-way ANOVAs revealed no significant differences in water temperature or Chl *a* between streams or years (Table 3), although no Chl *a* data were available for 2013.

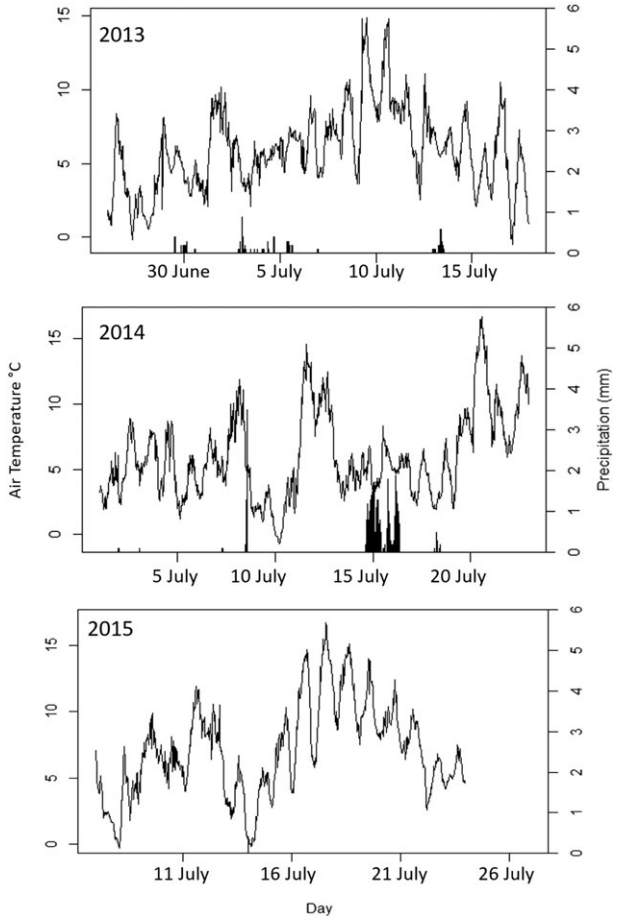

FIGURE 2 Mean air temperature and precipitation for the three field campaigns 2013 to 2015

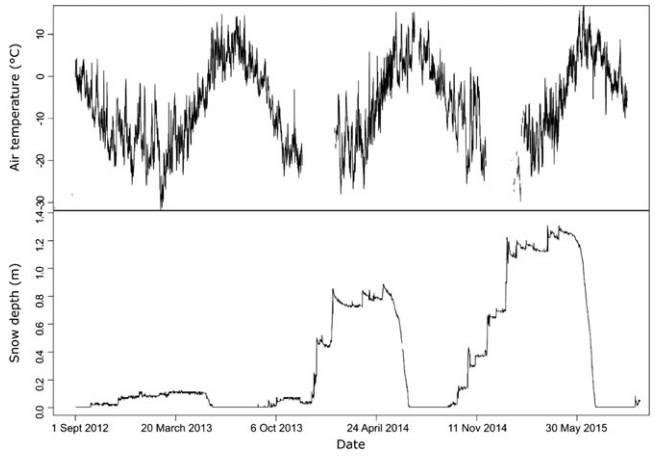

FIGURE 3 Air temperature and snow depth at Zackenberg valley over the 3-year study period between September 2012 and September 2015

3.2 | Macroinvertebrate community structure

Over the 3 years, 39 taxa were identified, of which 71.7% of the individuals were Chironomidae (29 taxa) and 26.5% were Oligochaetae. The remaining 1.8% comprised Ceratopogonidae, Simuliidae, Limoniidae, Musciidae, Sciaridae, Acari, Araneae, and Collembola (as can be seen in Table S1). Abundance varied between streams and year with the highest abundance found in Kærelv 2013 (4,335/m^2) and the lowest in Aucellaelv in 2014 (8/m^2). Taxa richness varied between 4 and 25 taxa per site (Figure 4). Interannual variability in evenness and Shannon diversity was greatest in Unnamed, Aucellaelv, and Palnatokeelv (Figure 5).

No significant difference was found for evenness or diversity between sites or years. Taxa richness was found to be significantly different between sites ($F(5,7) = 20.8$, $p < .001$) where a Tukey post hoc test found richness to be significantly higher in Kærelv and Grænseelv compared with Aucellaelv ($p < .01$), Palnatokeelv ($p < .01$), and Unnamed ($p < .05$). Taxa richness between Aucellaelv, Palnatokeelv, and Unnamed was not significant. However, macroinvertebrate abundance was significantly different between sites ($F(5,7) = 11.9$, $p < .01$) and years ($F(2,7) = 8.2$, $p < .05$). Kærelv and Grænseelv supported significantly higher abundance than Aucellaelv ($p < .01$), and Kærelv than Palnatokeelv and Unnamed ($p < .05$). Abundance was significantly higher in 2013 compared with 2015 ($p < .05$).

The ratio of Diamesa:Orthocladiinae was low and showed negligible variation in Kærelv and Grænseelv over the 3 years (mean: 0.3%, *SD*: 0.4), whereas in Unnamed, Palnatokeelv, and Aucellaelv, the ratio was high and also highly variable between sites and between years (mean: 91.0%, *SD*: 127.1; Table 1).

Oligochaeta were found in all sites in all years, however, abundance varied. The highest abundance was found in all sites during the 2013 field campaign, excluding Grænseelv when the highest abundance was found in 2014. Kærelv supported the highest abundance of all sites with 849/m^2 in 2013. The lowest abundance was found in 2015 for all sites apart from Aucellaelv (2014).

NMDS indicated the distinct grouping of the two most stable streams, closely distributed within the ordination space with negligible variation between them over the 3 years. In contrast, variation was large in the three unstable streams both interannually and between the sites (Figure 6). The NMDS reported a stress of 0.09. Only channel stability ($R^2 = 0.67$, $p < .01$) and bed sediment size ($R^2 = 0.62$, $p < .01$) were significantly correlated within the ordination. Channel stability increased and bed sediment size decreased towards the two more stable streams with the highest taxa diversity.

Along with channel stability and bed sediment size, community metrics were significantly correlated with other environmental variables (Table 4). Evenness was significantly correlated with climate variables (winter snow depth and summer air temperature both $r = 0.605$, $p < .05$). Shannon diversity was significantly correlated with conductivity and Mg concentration ($r = -0.57$, $p < .05$ and $r = -0.6$, $p < .05$, respectively) and taxa richness was significantly correlated with NO_3^- concentration ($r = -0.79$, $p < .01$).

Four indicator taxa were identified with values over 95%. These were Podonominae (Indicator value (Iv) = 100%, $p = .014$), *Corynoneura* (Iv = 99%, $p = .003$), *Hydrobaenus* (Iv = 98%, $p = .002$), and *Orthocladius* species types (Iv = 97%, $p = .002$) including *O. oliveri* type and *O.* G1 type. All indicator taxa were representative of high channel stability areas with small bed sediment size, and high macroinvertebrate abundance, diversity, and taxa richness. No indicator species were identified for low stability streams as taxa at these sites were also present in some stable streams even though *Diamesa* were found in high numbers in Aucellaelv and Palnatokeelv in 2013.

TABLE 1 Environmental variables and Diamesa:Orthocladiinae ratio during the three field campaigns (2013 to 2015)

Site	Year	Mean water temperature (n = 336 unless different below)		Channel stability (Pfankuch Index)	Suspended sediment		Bed sediment d_{50} (n = 100)		Water depth (n = 5 unless different below)		EC µS cm^{-1}	pH	Chl a (n = 5)		Diamesa: Orthocladiinae
		°C	*SD* (*n*)		Mg L^{-1}	*SD* (*n*)	mm	*SD*	cm	*SD* (*n*)			µg/m^2	*SD*	
Kærelv	2013	6.1	3.1	-	-	-	-	-	10	- (1)	192.2	-	-	-	0
	2014	5.7	2.5	-	5.1	0.0 (7)	-	-	20	3.9	55.1	-	504.49	233.7	0
	2015	6.1	2.7 (3)	74	-	-	51.2	6.6	21	7.9	36	7.0	392.69	125.8	1
Grænseelv	2013	7.3	2.5	-	-	-	-	-	3	- (1)	208	-	-	-	0
	2014	4.5	2.2	-	7.3	- (1)	-	-	16.8	2.3	54	-	336.16	236.3	0
	2015	3.7	1.8	78	-	-	33.9	2.7	14.4	9.4	32	7.1	198.52	90.8	0.8
Unnamed	2013	10	3	-	0.6	- (1)	-	-	2	- (1)	340	-	-	-	40
	2014	5.9	2.7	-	0.5	- (1)	-	-	20	2.4	-	-	327.29	140.2	0
	2015	1.4	1.0	113	-	-	90.3	4.9	7.6	4.5	42	7.0	503.97	301.9	8.7
Palnatokeelv	2013	10.1	- (1)	-	557.3	- (1)	-	-	5	- (1)	339	-	-	-	424.1
	2014	7.0	- (1)	-	96.3	- (1)	-	-	19	3.0	58.2	-	174.63	166.9	0
	2015	4.4	1.1 (3)	114	-	-	101.4	6.6	10.6	5.3	26	7.2	544.61	342.6	30
Aucellaelv	2013	6.4	2.7	-	463.1	- (1)	-	-	-	-	313	-	-	-	153.9
	2014	3.0	4.9	-	1120.3	0.6 (4)	-	-	16	4.2	127	-	165.53	238.4	100
	2015	0.8	0.6	116	-	-	96.5	5.7	12.8	4.9	88	7.0	289.94	149.7	62.5

Note. EC = electrical conductivity; Chl a = Chlorophyll *a*; *SD* = standard deviation; *n* = number of samples; - = data not available.

TABLE 2 Water chemistry data for stream sites over the three field campaigns

		Mg^{2+} (µEq L^{-1})		Na^+		K^+		Ca^{2+}		Si mg/L		NH_4^+ (µEq L^{-1})		NO_3^-		PO_4^{3-}	
Site	*n*	M	*SD*	M	*SD*	M	*SD*	M	*SD*	M	*SD*	M	*SD*	M	*SD*	M	*SD*
Kærelv 2013	1	122.6	NA	143.4	NA	24.15	NA	641.3	NA	2.2	NA	NA	NA	NA	NA	NA	NA
Kærelv 2014	6	64.6	16.9	143.9	171.5	14.7	7.2	195.0	50.1	1.1	NA	1.1	0.8	0.0	0.1	0.3	0.4
Kærelv 2015	3	50.1	4.5	64.4	8.2	13.0	3.5	144.2	20.3	1.3	0.11	0.8	0.2	0.1	0.1	0.1	0.01
Grænseelv 2013	1	266.7	NA	321.6	NA	48.2	NA	728.7	NA	2.0	NA	NA	NA	NA	NA	NA	NA
Grænseelv 2014	4	54.3	13.4	41.4	11.9	9.6	2.7	143.3	37.7	1.1	NA	0.4	0.1	0.01	0.01	0.1	0.01
Grænseelv 2015	3	38.4	20.9	36.8	14.9	10.3	4.5	102.9	41.6	1.3	0.2	3.1	3.1	0.04	0.02	0.1	0.02
Unnamed 2013	1	291.7	NA	130.0	NA	29.7	NA	1504.8	NA	1.75	NA	NA	NA	NA	NA	NA	NA
Unnamed 2014	3	138.1	44.4	42.0	16.2	13.2	3.8	586.5	292.7	1.2	NA	0.4	0.1	0.0	0.01	0.1	0.01
Unnamed 2015	3	38.0	6.0	39.1	5.2	10.7	1.5	157.1	16.6	1.0	0.1	0.7	0.1	0.1	0.6	0.1	0.00
Aucellaelv 2013	1	345.8	NA	592.6	NA	42.8	NA	933.3	NA	2.0	NA	2.4	0.4	1.80	0.2	0.1	0.04
Aucellaelv 2014	3	211.0	62.8	305.8	62.9	26.1	3.4	460.2	118.6	2.2	NA	1.9	0.4	0.8	0.2	0.1	0.05
Aucellaelv 2015	3	88.6	18.4	148.8	23.6	5.3	0.6	227.8	30.0	0.8	0.1	1.1	0.1	0.4	0.2	0.1	0.02
Palnatokeelv 2013	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Palnatokeelv 2014	2	71.46	2.29	66.96	4.35	10.38	0.38	164.25	15.5	1.23	NA	0.69	0.23	0.19	0.12	0.13	0.03
Palnatokeelv 2015	3	38.60	10.05	19.52	16.51	4.16	3.51	102.46	13.4	0.95	0.11	1.06	0.27	0.69	0.26	0.10	0.03

Note. M = mean, *SD* = standard deviation, *n* = number of samples.

The two-way cluster analysis also highlighted high macroinvertebrate abundance in stable streams, particularly in 2013, and the distance between *Diamesa* spp. and *D. aberrata* compared with all other taxa, emphasizing the different environmental conditions in which they are found (Figure 7). Abundance of *Diamesa* increased in streams with lower channel stability and increased bed sediment size.

4 | DISCUSSION

Macroinvertebrate community structure was significantly different between streams with small snowpacks compared with streams with large snowpacks, and between the 3 years. Channel stability and bed sediment size were the best predictors for macroinvertebrate community dynamics as indicated by ordination and Spearman's rank correlation.

4.1 | Variation in environmental habitat conditions

The influence of water source on stream physicochemical habitat has been well documented (e.g., Blaen et al., 2014; Brown et al., 2003; Parker & Huryn, 2011; Ward, 1994). However, past research has typically focused on the comparative influence of different water source

TABLE 3 Two-way ANOVA results for environmental variables with site and year

Variable	Site	Year	Site*Year
Water temperature	-	-	-
Chl *a*	-	-	-
EC	-	$F(1,4) = 28.54$, $p = <.01$	-
NH_4	-	-	-
NO_3	$F(1,4) = 22.50$, $p = <.05$	$F(1,4) = 11.03$, $p = <.05$	-
PO_3	-	-	-
Si	-		-
Ca	$F(1,4) = 7.33$, $p = <.05$	$F(1,4) = 58.54$, $p = <.01$	-
Mg	$F(1,2) = 6.83$, $p = <.05$	$F(1,4) = 56.57$, $p = <.01$	-

Note. EC = electrical conductivity; Chl a = Chlorophyll *a*; - = no significant difference.

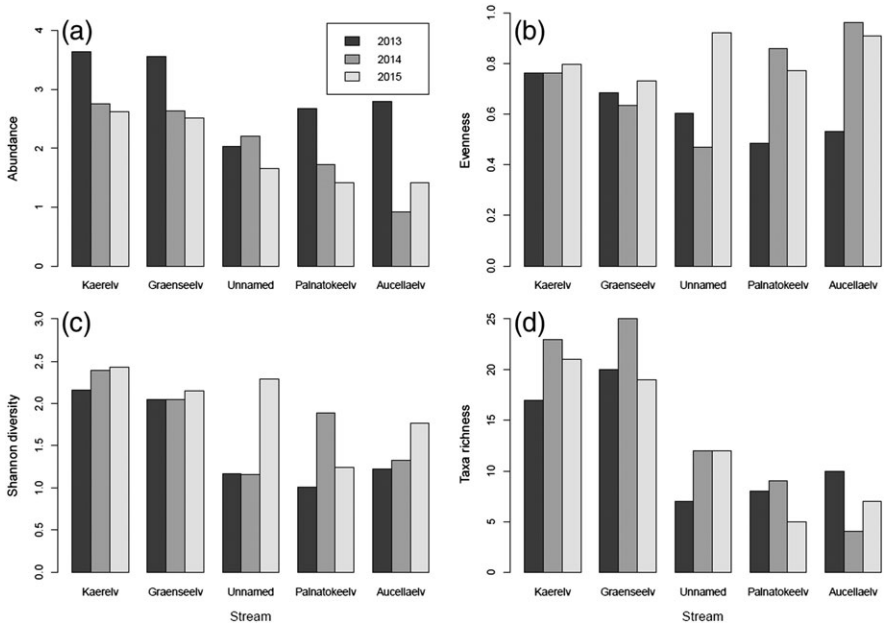

FIGURE 4 Bar charts showing (a) Abundance (individuals/m^2 log10(x + 1) transformed), (b) Evenness, (c) Shannon diversity index, and (d) Taxa richness

types (glacier, snow, and groundwater) and less so on variation in influence within one water source type. Streams in the Zackenberg region sourced from large, perennial snowpacks (Aucellaelv, Palnatokeelv, and to a lesser extent Unnamed) were characterized by low channel stability and high suspended sediment concentration compared with streams from smaller, seasonal snowpacks (Kaerelv, Graenseelv). These findings support Hypothesis 1 that streams sourced from larger snowpacks would have reduced channel stability and increased disturbance.

The traditional model for snowmelt-dominated streams states that they are characterized by low turbidity due to transporting low levels of sediments, although turbidity can be elevated during high flow (Milner & Petts, 1994; Brown et al., 2003), and that their hydrochemistry is determined by the release of ions from melting snowpacks (Brown et al., 2003; Malard, Tockner, & Ward, 1999). Kærelv and Grænseelv, the two streams with seasonal snowpacks, and also Unnamed, the stream fed by both seasonal and perennial snowpacks, met the definition in this model, however, Aucellaelv and Palnatokeelv did not. Aucellaelv and Palnatokeelv demonstrated hydrochemistry related to soil erosion more than ionic release from snowpacks. High turbidity and channel mobility was standard in these two streams, where Aucellaelv moved by 1 m during a heavy precipitation event in 2014 (personal observation) and formed a large thermo-erosional tunnel in 2015 (Docherty, Hannah, Riis, Rosenhøj Leth, & Milner, 2017a). The high variability in conductivity and solute load between sites is representative of the different levels of fluvial erosion and nivation processes taking place at each site (Hasholt & Hagedorn, 2000), leading to high suspended sediment concentrations in streams, which are then weathered in-stream by turbulent flow, releasing ions and nutrients (Chin et al., 2016). Previous research has shown all streams in this study to have low nutrient and dissolved organic carbon concentrations and low primary producer biomass, with nutrient uptake being low as a result (Docherty, Riis, Hannah, Rosenhøj Leth, & Milner, 2018).

In the Zackenberg region, the largest snowpacks generally accumulate on south facing lee slopes following northerly winds blowing snow and sediment into ridges and fluvial terraces (Christiansen, 1998). Although under future scenarios of increased snowfall, all areas would receive more snow. However, these larger snowpacks could be expected to cause more extreme spring flood events at the onset of snow melt (Dankers & Middelkoop, 2008), destabilising stream bed and the nearby floodplain sediment, increasing channel mobility, and

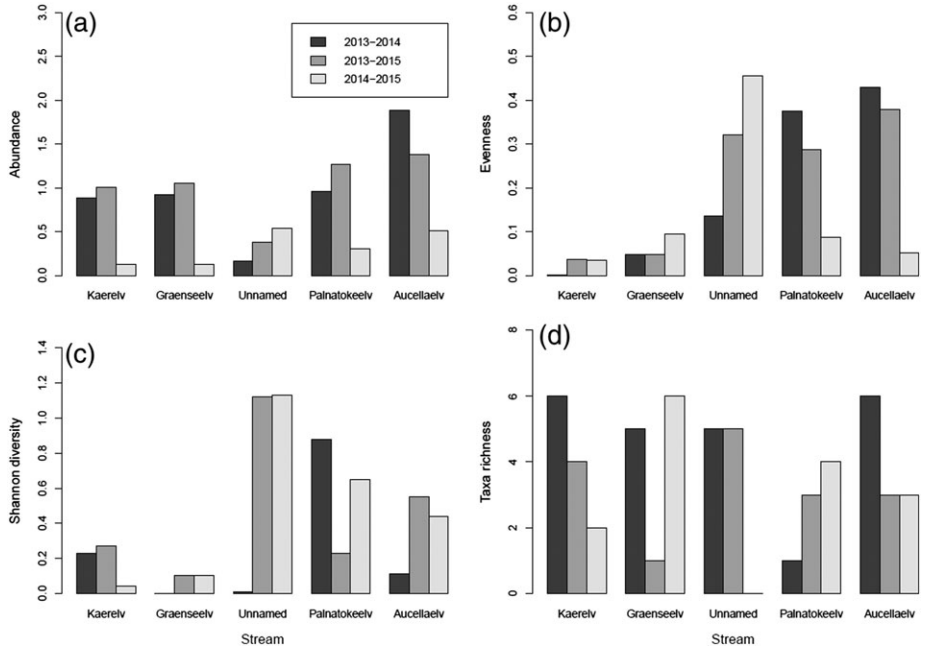

FIGURE 5 The difference between years in community metrics per site. Note largest difference in Evenness and Shannon diversity in the streams Unnamed, Palnatokeelv, and Aucellaelv

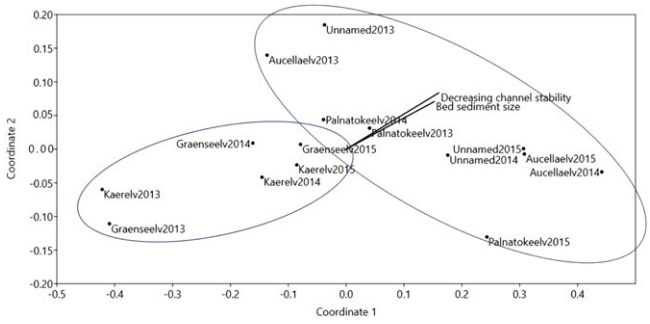

FIGURE 6 Nonmetric multidimensional scaling of sites with significant environmental variables plotted. Circles show streams sourced from small seasonal snowpacks (Kærelv and Grænseelv) and from large perennial snowpacks (Unnamed, Aucellaelv, and Palnatokeelv)

uprooting vegetation. The variation in snow accumulation throughout the landscape leads to large spatial variation in ground thermal regime by snow cover acting as an insulator between ground and air (Westermann et al., 2015), leading to different permafrost degradation and active layer depth locally, and subjecting streams in close proximity to one another to different pressures based on local geomorphology. As well as snowfall, streams could see increased disturbance due to increased summer rain events. In summer, rain events in the Arctic are known to have large influences on streams by increasing sediment load, inundating floodplains and causing rapid mass movements (Cogley & McCann, 1976; Lamb & Toniolo, 2016; Lewis, Braun, Hardy, Francus, & Bradley, 2005).

Environmental conditions in streams were markedly different in 2013 compared with 2014 and 2015 due to the unusually low snow depth during the previous winter, reducing snow melt inputs to all streams. Low water levels caused higher solute concentrations due to solutes constituting a larger fraction of the water body, and some stream reaches of Kærelv and Grænseelv constituted mainly of pools with limited surface water connectivity. Even though ionic load and suspended sediment concentration was found to be highly variable between sites and years¸ this was not found to have a significant impact on Chl *a* concentration. However, Chl *a* data were not available from 2013, when habitat conditions were most contrasting, and as biofilms form an important food source for macroinvertebrates, this could have provided interesting insights into macroinvertebrate abundance variability. The different time periods each year could have been a factor influencing variation between years due to variation in air temperature and timing of onset of snowpack melting, as air temperature was notably colder in the 2013 field campaign (June) compared with that in 2015 (July). However, the large variation in snow depth throughout the three winter seasons is believed to have a much larger influence than the 2-week difference in field campaign onset timing.

4.2 | The relationship between benthic macroinvertebrate communities and environmental habitat variables

Macroinvertebrate abundance and taxa richness varied between streams, with the most stable streams Kærelv and Grænseelv supporting higher densities and richness than Unnamed, Aucellaelv, or Palnatokeelv. Spatial variation in abundance and taxa richness was found to be correlated with channel stability and bed sediment size, supporting Hypothesis 2, that lower channel stability will lead to reduced macroinvertebrate taxa richness and abundance, but not supporting the hypothesis that it will also lead to reduced diversity. Several taxa, found in low numbers, were only found in the most stable streams including *Thienmaniella clavicornis*, *Orthocladius* G1, and *Krenosmittia*, highlighting the importance of these streams for local diversity. Four indicator taxa characteristic of stable snowmelt streams

TABLE 4 Spearmans rank correlation coefficients for community metrics from all streams and years with environmental variables

	Abundance *r*	Evenness *r*	Shannon diversity index *r*	Taxa richness *r*
Channel stability	**−0.57***	-	**−0.7****	**−0.83****
Temperature	-	-	-	-
Chl a	-	-	-	-
EC	-	-	**−0.57***	-
Suspended sediment	-	-	-	-
pH	-	-	-	-
Water depth	-	-	-	-
Bed sediment size	**−0.51***	-	**−0.61***	**−0.83****
Mean winter snow depth	**−0.62***	**0.605***	**-**	**-**
Mean air temperature	**−0.624***	**0.605***	**-**	**-**
NH_4	-	-	-	-
NO_3	-	-	-	**−0.79****
PO_3	-	-	-	-
Si	-	-	-	-
Ca	-	-	-	-
Mg	-	-	**−0.6***	-

Note. EC = electrical conductivity; Chl a = Chlorophyll *a*; - = no significant difference.

*$p < .05$,

**$p < .01$.

in this region were identified, which were Podonominae, *Corynoneura*, *Hydrobaenus*, and *Orthocladius*. The streams sourced from seasonal snowpacks demonstrated low channel mobility, relatively stable water levels (field observations), low suspended sediment concentration, and small bed sediment size, creating a stable environment for macroinvertebrate communities. In contrast, streams with perennial snowpack sources had high channel mobility, large bed sediment size, and, apart from Unnamed, high suspended sediment concentration. High suspended sediment concentration is known to have a large negative impact on macroinvertebrate communities for a number of reasons, including increasing invertebrate drift through substrate instability; affecting respiration through silt accumulation on respiratory organs and through reducing water oxygen concentration; and by reducing food availability by reducing biofilm growth (Eriksen, 1968; Lemly, 1982; Peckarsky, 1984; Wood & Armitage, 1997). Previous research has also found longitudinal variation in macroinvertebrate abundance within these streams, where variation in ionic enrichment of water due to snowmelt inputs lead to variation in biofilm biomass consequently impacting macroinvertebrate communities (Docherty, Hannah, Riis, Rosenhøj Leth, & Milner, 2017b).

Bed sediment provides refuge from disturbances and predation, for feeding and for egg deposition for macroinvertebrates (Brusven & Rose, 1981; Dole-Olivier, Marmonier, & Beffy, 1997; Gayraud & Philippe, 2003; Palmer, Bely, & Berg, 1992). Large heterogeneity in bed sediment size, for example, a combination of large cobbles and silt, causes interstitial spaces to become blocked (Gayraud & Philippe, 2003), reducing macroinvertebrate habitat and making them unsuitable for certain taxa (Erman & Ligon, 1988; Richards & Bacon, 1994). In this study, streams with large bed sediment supported reduced macroinvertebrate abundance, diversity, and taxa richness, and two of the three streams with large sediment size also showed the largest suspended sediment concentrations, leading to increased sediment size heterogeneity and reduced interstitial spaces for invertebrates.

Water temperature in this study was not significantly different between sites or years. Warmer water temperature causes higher metabolic demands of both individuals and ecosystem as a whole (Brown, Gillooly, Allen, Savage, & West, 2004), and water temperature and channel stability are considered the best predictor of

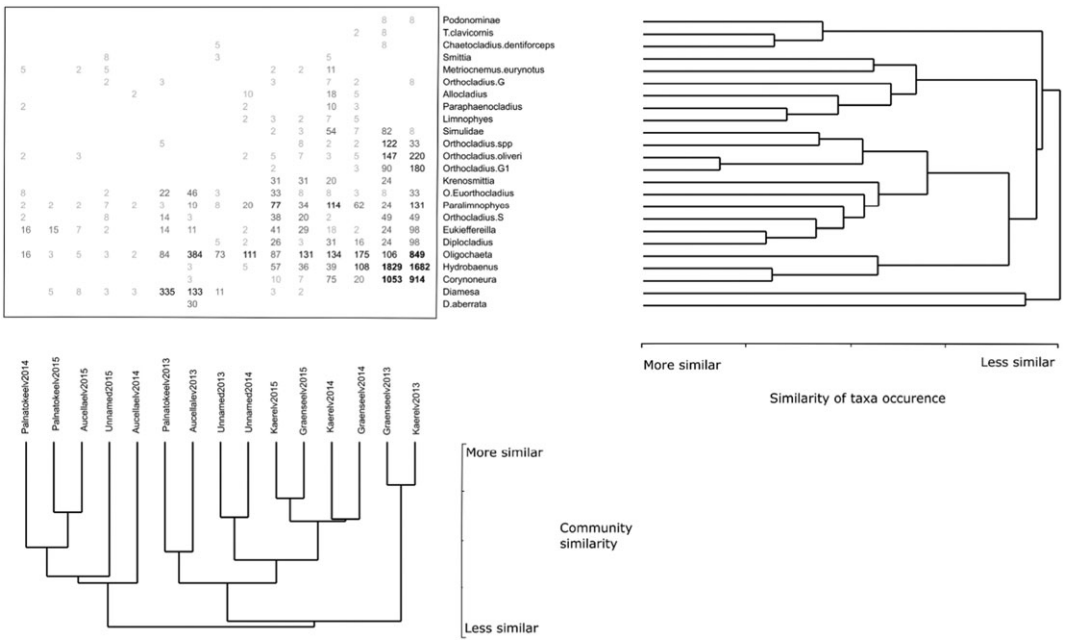

FIGURE 7 Two-way cluster analysis showing similarity between streams and taxa. Kærelv and Grænseelv, which have the highest macroinvertebrate abundance, are shown to be least similar to Aucellaelv and Palnatokeelv, which have the lowest macroinvertebrate abundance

macroinvertebrate community composition in glacially influenced rivers (Milner, Brittain, Castella, & Petts, 2001; Milner & Petts, 1994). Along with channel stability, water temperature has been found to be the habitat variable that best explains macroinvertebrate community composition (Friberg, Milner, Bergfur, Rasmussen, & Sandin, 2013) and taxa richness (Castella et al., 2001; Friberg et al., 2001), and in alpine regions, increased water temperature has been found to cause decreases in beta diversity (Finn, Khamis, & Milner, 2013). Although other studies in Arctic and alpine regions find significant variation in water temperature between streams and sites due to variations in water source contributions (e.g., Blaen, Hannah, Brown, & Milner, 2013; Cadbury, Hannah, Milner, Pearson, & Brown, 2008; Mellor, Dugdale, Garner, Milner, & Hannah, 2016), the similarity between the streams in this study in terms of their water source limits variation in water temperature, where variation maybe more due to stream size and consequently, the time needed to warm up.

Macroinvertebrate abundance and evenness was found to be significantly correlated with winter snow depth, supporting Hypothesis 3, that streams sourced from larger snowpacks will see higher interannual variability in community structure between years of different snowfall amount. Given this correlation, the interannual variation in snow depth and associated variation in stream habitat is likely the principal contributing factor causing interannual variation in macroinvertebrate community structure.

Low water levels typically result in decreased abundance, but higher overall abundances can also be found where water levels are reduced, both due to changes in habitat suitability and food resources (Dewson, Death, & James, 2003; Dewson, James, & Death, 2007; Epele, Miserendino, & Brand, 2012; Gore, 1977; Wright & Bernie, 1987; Wright & Symes, 1999). Of the four indicator taxa identified for high stability streams, Podonominae was found only in stable streams in 2013, when water level was at its lowest, *Corynoneura*, *Hydrobaenus*, and *Orthocladius* spp., the other three indicator taxa, also had the greatest densities in 2013, when *Hydrobaenus* was dominant followed by *Corynoneura*. These genera have been found previously to peak in abundance during low flow periods in Patagonian streams (Epele et al., 2012).

Although some chironomids are thought to have a long larval stage in cold regions before emergence, the large interannual variation in abundance is not expected to be explained through this mechanism. Orthocladinae and Diamesiinae, the principal Chironomidae subfamilies present, are known to be adapted to cold environments (Lindegaard, 1995; Milner & Petts, 1994) and to have a degree of flexibility in their developmental rate dependent upon habitat conditions (Ferrington & Mastellar, 2015). Water temperature regimes have been found to be important to developmental rate, where developmental period of *Diamesa mendotae* have been shown to be the shortest at low temperatures, being 63 days at 4–6 °C, but 93 days at 8–10 °C (Bouchard & Ferrington, 2009; Ferrington & Mastellar, 2015). *Diamesa mendotae*, *Diamesa incallida*, and *Diamesa cheimatophila* are all thought to produce more than one generation during a season (Ferrington & Mastellar, 2015). The low variation in water temperature between years and sites and the adaptive nature of Arctic macroinvertebrates to cold environments implies that habitat conditions in this study should not be restricting factors for larval development.

4.3 | Zackenberg in a global context

Mean macroinvertebrate abundance was low at Zackenberg (747/m^2) when compared with west Greenland, where mean abundance was 1,113 individuals/m^2 in streams with weak glacial influence (Friberg et al., 2001). However, taxa richness was found to be higher at Zackenberg (13.3) compared with on the west coast (10.5 in streams with weak glacial influence; Friberg et al., 2001). When compared with streams of all water sources on the west coast, higher taxa diversity was found in west Greenland streams compared with Zackenberg. At Zackenberg, taxa were restricted to the order Diptera and Oligochaeta, whereas on the west coast in streams either sourced from groundwater or downstream of lakes, taxa also included Ephemeroptera, Trichoptera, and the snail *Lymnaea* sp. (Friberg et al., 2001; González-Bergonzoni et al., 2014). Despite these differences, *Hydrobaenus* was found to be one of the most abundant genera (Friberg et al., 2001) similar to this study from northeast Greenland. The more southern location in the low Arctic climate zone and the proximity to mainland Canada may explain the higher diversity present in West Greenland, as diversity is known to decrease with increasing latitude for all aquatic taxa apart from Chironomidae (Böcher et al., 2015). Coastal Greenland has been ice-free since the Pleistocene glaciation 10,000 years BP (Bennike, 1999; Böcher et al., 2015). Due to the short-time frame invertebrates have had to colonize the region, combined with the isolation of the east coast of Greenland, where dispersal routes are either from Canada, crossing the harsh climatic conditions of north Greenland or across oceans (Böcher et al., 2015), taxa diversity is low in this region. However, there is evidence that ice-free areas may have existed along the east coast during the last glaciation even though average air temperatures were 23 °C lower than present, which may have acted as refugia for some invertebrate species (Böcher et al., 2015; Dahl-Jensen et al., 1998; Funder, 1978; Funder, 1979). Streams at Zackenberg had restricted diversity compared with streams in eastern Canada, where 92 species types of Chironomidae were found in rivers of different water sources (nival, glacial, and lake fed) between 58 and 82°N (Namayandeh, Heard, Luiker, & Culp, 2016), and compared with a glacial stream in Iceland, where macroinvertebrate communities included Chironominae, Plecoptera, and Trichoptera as well as other Diptera (Gíslason et al., 2001). However, macroinvertebrate abundance at Zackenberg was found to be much more variable between streams compared with those in Svalbard, where abundance varied between 446 individuals/m^2 and 1,558 individuals/m^2 in streams of varying water sources (glacial melt, snow melt, and groundwater; Blaen et al., 2014).

5 | IMPLICATIONS OF CLIMATE CHANGE ON ARCTIC STREAM ECOSYSTEMS

Most research on the impact of climate change on Arctic streams has been focused on a shift from glacial (unstable) to groundwater or snowmelt (stable) streams. This paper presents the opposite scenario where streams decrease in channel stability through increased snowmelt water inputs, and so provides novel insights into future ecosystem dynamics in Arctic streams. Under this proposed scenario, streams are suggested to support lower macroinvertebrate abundance

and diversity, and for there to be higher variability both between streams and interannually dependent on the size of the snowpack. This could provide favourable conditions for taxa adapted to unstable environments, such as *Diamesa*, but could potentially result in the local extinction of rare species types that are only able to inhabit stable streams (e.g., *Trichotanypus*), and reductions in numbers of many present common taxa such as *Hydrobaenus* and *Corynoneura*.

This research shows the large variation in climate change pressures upon streams within a small area, and highlights the need for increased research efforts on snowmelt streams to understand the different dynamics. The interannual variation in habitat variables and community metrics highlights the importance of long-term studies for a full understanding of stream dynamics.

The different environmental and climatic conditions in this region compared with other Arctic locations mean that the response of stream ecosystems to a changing climate in ice-free northeast Greenland is expected to be different to that of other Arctic regions. However, previous research has predicted increased snowfall in parts of north Russia and associated peaks in stream discharge during spring floods (Dankers & Middelkoop, 2008), which could see similar patterns on stream habitat and macroinvertebrate communities to those predicted in this paper for northeast Greenland. Further research is required to see if this model is applicable to other Arctic regions.

ACKNOWLEDGEMENTS

Catherine Docherty was funded by a Natural Environment Research Council (NERC) studentship (NE/L501712/1). Fieldwork to Zackenberg was funded through the European Union Seventh Framework Programme (FP7/2007–2013) under Grant agreement 262693 (INTERACT) and by Carlsberg Foundation (2013-01-0258; Tenna Riis). Precipitation data from the Greenland Ecosystem Monitoring Programme were provided by Asiaq—Greenland Survey, Nuuk, Greenland. Other climate data from the Greenland Ecosystem Monitoring Programme were provided by the Department of Bioscience, Aarhus University, Denmark, in collaboration with Department of Geosciences and Natural Resource Management, Copenhagen University, Denmark. The authors thank Biobasis, Geobasis, and Zackenberg logistics for all of their field assistance and Andy Moss and Steve Brooks for their assistance in Chironomidae identification. The authors thank John Brittain, Stefan Krause, and two anonymous reviewers for providing comments on the manuscript. We thank Chantal Jackson for Figure 1.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

How to cite this article: Docherty CL, Hannah DM, Riis T, Lund M, Abermann J, Milner AM. Spatio-temporal dynamics of macroinvertebrate communities in northeast Greenlandic snowmelt streams. *Ecohydrology*. 2018;e1982. https://doi.org/10.1002/eco.1982